Takasi YAMAZAKI*: **Endosperm formation of *Lindenbergia philippensis* (Scrophulariaceae) and the systematic position of the genus**

山崎 敬*: *Lindenbergia philippensis* (ゴマノハグサ科)の胚乳形成および属の分類上の位置

The embryological investigations of the genus *Lindenbergia* are very scanty. The endosperm formation of this genus has been reported by Hartl (1957) and Banerji (1961), but their reports are brief and modificatory. Therefore, it is proposed to study the embryo sac and the endosperm formation of *L. philippensis* (Cham.) Benth.

The material was collected from Sai Yok—Nam Tok, Kanchanaburi, Thailand in Aug. 1983 by the author, and fixed in F. A. A. It was dehydrated in tertiary butyl alcohol series and embedded in paraffin. Serial longitudinal and transverse sections of 12 μm thickness were stained in Haidenhain's Iron Haematoxylin.

Observations Nucellus consists of a single layer of epidermal cells surrounding single archesporial cell (Fig. 1. 1). The archesporial cell enlarges considerably and directly functions as the megaspore mother cell (Fig. 1. 2). This cell undergoes meiotic divisions and produces linear tetrad of megasopres (Fig. 1. 3). Three micropylar megaspores degenerate and the chalazal one is functional (Fig. 1. 4). The functional megaspore undergoes three nuclear divisions and develops into 8-nucleate embryo sac stages (Fig. 1. 5, 6). The nuclei divide once again to produce eight nuclei which organize into 3-celled egg apparatus and 3-antipodal cells arranging in a line, while remaining two fuse in the center forming a secondary nucelus (Fig. 1. 7). This type of embryo sac formation is known as monosporic Polygonum-type. At the time of megaspore tetrad formation, the nucellar layer almost degenerates and the inner layer of the integument becomes differentiated as endothelium. At mature embryo sac stage the endothelium covers the chalazal half of the embryo sac (Fig. 2. 1).

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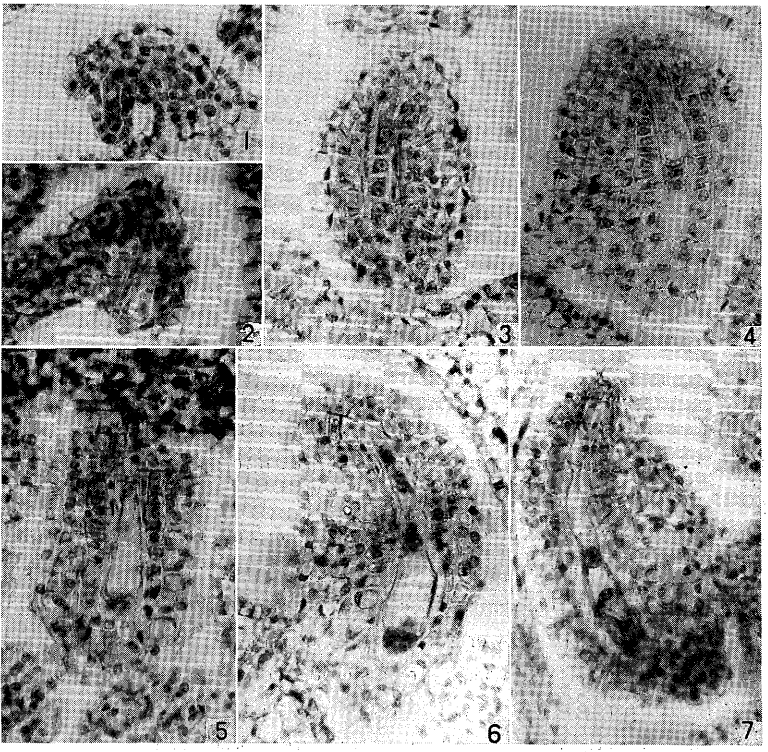

Fig. 1. Megaspores and embryo sac formations. 1. Single archesporial cell. 2. Megaspore mother cell. 3. Tetrad of megaspores. 4. Basal megaspore functioning, upper three degenerating. 5. Four-nucleate embryo sac. 6. Eight-nucleate embryo sac. 7. Embryo sac after fertilization. All ×350.

The primary endosperm nucleus is situated at the middle of the embryo sac and divides. A transverse wall follows this division to form a two-celled endosperm. The chalazal cell does not divide further and functions directly as a chalazal haustorium which is formed by one cell with one nucleus (Fig. 3. 2). One subsequent transverse division occurs in the micropylar cell, and results in a row of three cells, a chalazal cell, a central cell and a micropylar cell (Fig. 2. 2). The micropylar cell enlarges and divides longitudinaly to form two juxtaposed cells. Without being followed by wall formation a nuclear division occurs in these two cells. These enlarged and bi-nucleate cells function as the micropylar

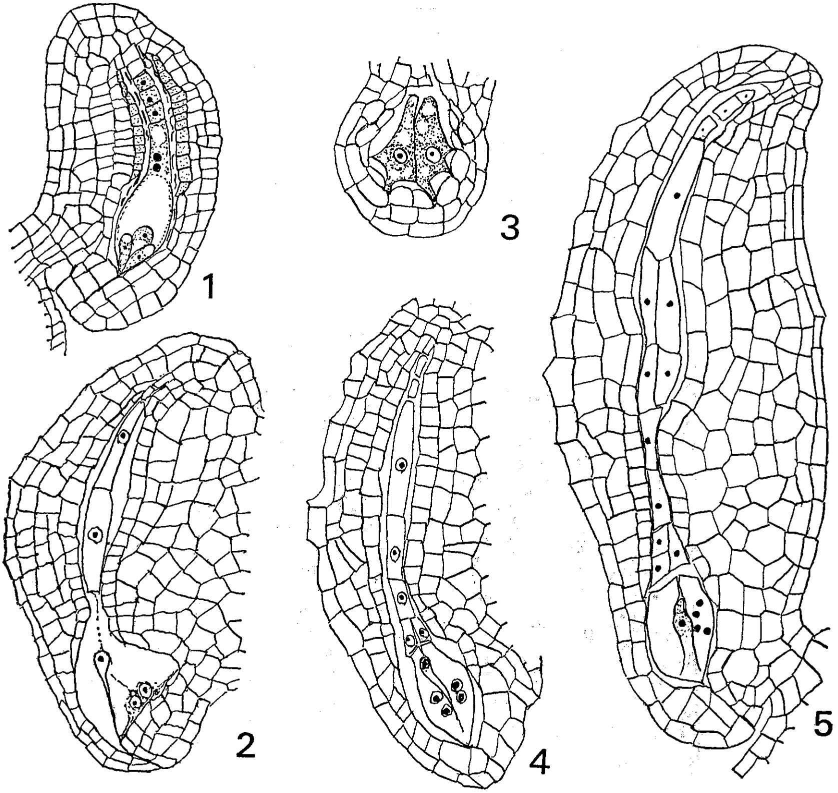

Fig. 2. Endosperm formation. 1. Pre-fertilized embryo sac. 2. Four-celled endosperm, the micropylar haustorium has two cells with one nucleus each. 3. Transverse section of micropylar haustorium. 4. Young endosperm showing a linear row of one- or two-celled tiers. Micropylar haustorium has two cells with two-nuclei each. 5. Young endosperm showing a linear row of one- or two-celled tiers. Micropylar haustorium is one cell with four nuclei All ×350.

haustorium (Fig. 2. 3, 4). The separating membrane of the micropylar haustorium is very thin and its early dissolution results in the formation of a single bulbous body with 4-nuclei (Fig. 3. 1, 3). The middle cell of the three-celled endosperm undergoes a seris of transverse and scantily longitudinal divisions, and gives rise to a linear endosperm with 5–10 tiers having one or two cells each (Fig. 2. 4, 5 and 3. 1). By further transverse and longitudinal divisions the cells of the linear endosperm form the many-celled and oblong endosperm proper (Fig.

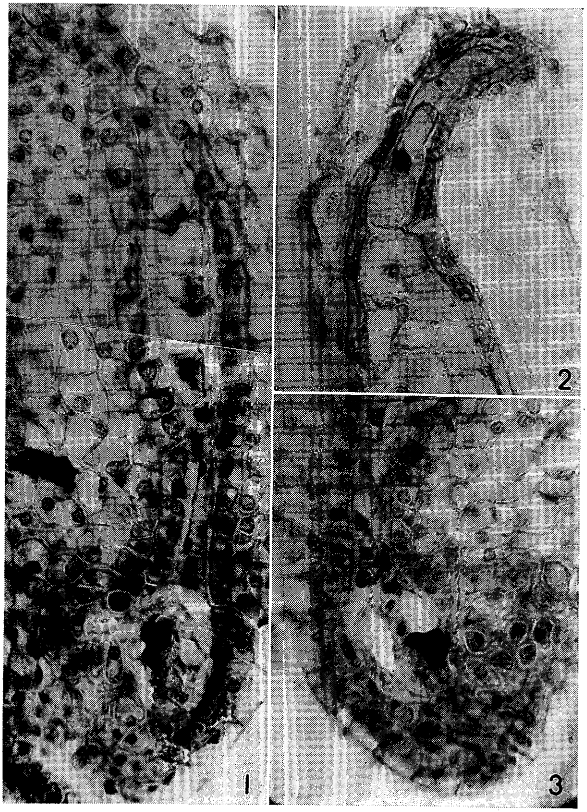

Fig. 3. 1. Young endosperm with many one-celled tiers. 2. Chalazal haustorium being uni-nucleate one cell. 3. Micropylar haustorium being one cell with four-nuclei. All ×350.

4. 1). The cells of 3 or 4 tiers toward the micropylar part of the linear endosperm do not divide longitudinally except one or two cells being in contact with the micropyle. The latter cells form a linear stalk with about 10 cells between the micropylar haustorium and the endosperm proper (Fig. 4. 1).

As the seed approaches maturity, the chalazal haustorium disintegrates. The micropylar haustorium appears spongy in texture and stains darkly (Fig. 4. 3). The cells of the epidermis of the integument show the thickening cell-walls. The endothelial cells enlarge and develop a cuticle on their inner and radial

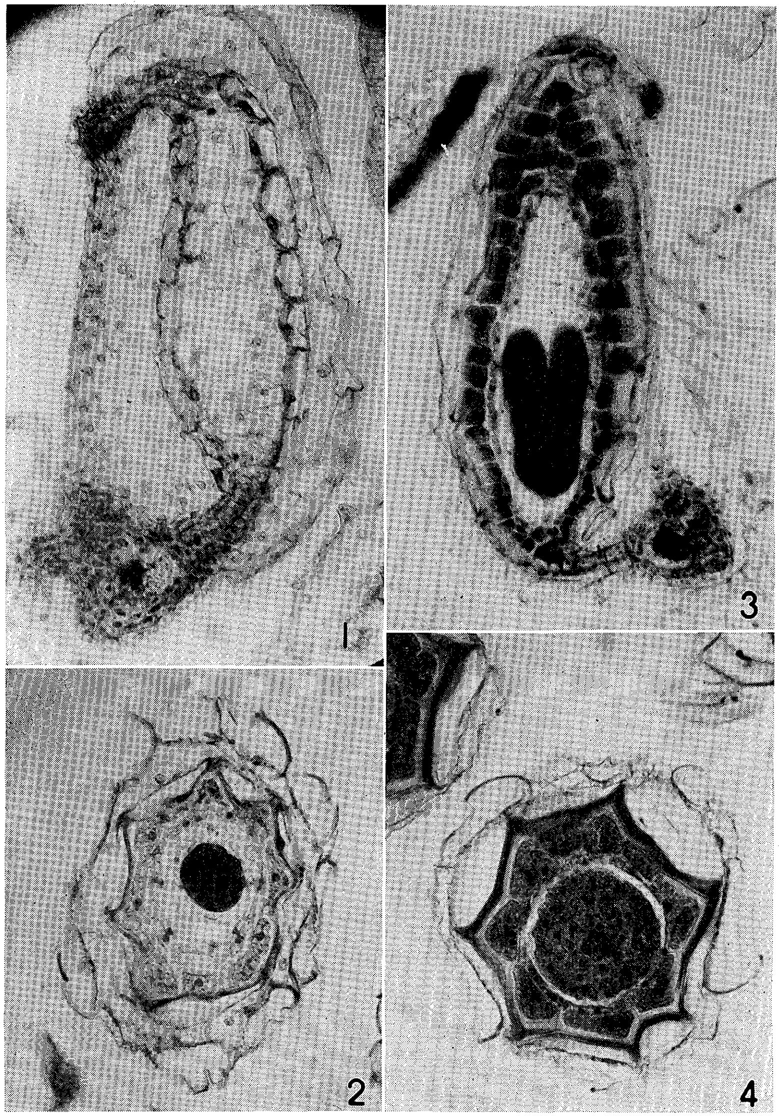

Fig. 4. 1. Vertical section of ovule showing enlarged endotherial cells. 2. Transverse section showing epidermal cell-walls of integument and endotheral ones thickening. 3. Vertical section of young ovule. 4. Transverse section of ovule showing inner and radial walls of endotherial cells much cuticlized. 1 ×200, 2 and 4 ×190, 3 ×150.

walls. The integumentaly cells between the endothelial layer and the epidermis gradually break down and disintegrate completely at the mature seed (Fig. 4. 2, 3). The mature seed consists of a straight embryo with two equal cotyledons surrounded by one layer of the endosperm cells packed with starch and the seed coat. The seed coat is made up of the endothelial layer, in which the cells have much cuticlized inner and radial walls, and the partially broken-down epidermis of the integument (Fig. 4. 4).

Discussion In *Lindenbergia philippensis*, the chalazal haustorium is a uninucleate cell, simple, and penetrates into the hypostase region. The micropylar haustorium develops from two cells having bi-nuclei each. The separating membrane of micropylar haustorium is very thin and soon dissolves to result in the formation of a single bulbous body with 4 nuclei. The endosperm of this type, in which it has a single uninucleate chalazal haustorium and a single 4-nucleate micropylar haustorium derived from two cells, is reported for *Limnophila heterophylla* (Krishna Iyengar 1939), *Stemodia viscosa* (Krishna Iyengar 1939, Srinivasan 1940), *Torenia fournieri* and *T. violacea* (Guilford & Fisk 1951, Yamazaki 1955). Several authors (Glisic 1936, Crété 1951, Banerji 1961) have typified for various forms of the endosperm haustoria of the Scrophlariaceae and tried to show the phylogenetic relationships. These reports suggest that the phylogenetic value on the haustorial types would be useful in considering the relationship between the species in a genus or among allied genera, though not effective in the tribes or the subfamilies with a exception of the tribe Rhinantheae. Therefore, the similar type of the haustoria as seen in *Lindernia, Torenia, Limnophila, Stemodia* and *Lindenbergia* is not necessarily to show the phylogenetic relationships.

In early endosperm formation of *Lindenbergia philippensis*, the middle cell of three-celled endosperm stage divides transversally, and the following several divisions are generally transversal to form a linear row of 6–10 tiers having one or two cells each. The developed endosperm proper has a stalk toward the micropylar part. The similar appearances as above are observed in *Sopubia delphinifolia* and *S. trifida* (Krishna Iyengar 1937, 1940), *Rehmannia angulata* (Krishna Iyenger 1942) and *Gratiola japonica* (Yamazaki 1953). The chalazal and micropylar haustoria develop poorly in *Gratiola japonica*. In the species of *Sopubia* the endosperm proper has no stalk. *Rehmannia angulata* shows the most similar endosperm formation to that of *Lindenbergia philippensis*.

In the tribe Gratioleae the lower lobes of the corolla are covered by the upper ones. This aestivation of the corolla is one of the important characters of the subfamily Scrophularioideae. However, the genus *Lindenbergia* has the different aestivation that the upper lobes of the corolla covered by the lower ones. This aestivation is one of the importaht characters of the subfamily Rhinanthoideae. Hartl (1957) indicated that the aestivation of the corolla was not necessarily to show the phylogenetic relationship in the Scrophulariaceae and has concluded that the genus *Lindenbergia* should belong to the tribe Gratioleae. He advocated a new system of the Scrophulariaceae without attaching importance for the corolla-aestivation (Hartl 1965). However, the aestivation of the corolla is related with the lower lip having a tendency to enlarge, and seems to be a important character for the purpose to produce a foothold for the insect in pollination.

In the most genera of the tribe Gratioleae the stigma is bilamellate. In many genera of this tribe as *Lindernia, Torenia, Mazus, Limnophila, Dopatrium* and *Mimulus,* the lamellae of stigma are widely open each other in the pre-fertilized flower, and as soon as the inner side of the lamella is touched, the lamellae snap together. On the other hand, in the genus *Lindenbergia* the stigma is capitate and has no relation with the above mentioned movement.

By the characters of the endosperm formation, the aestivation of the corolla and the capitate stigma, it can be concluded that the genus *Lindenbergia* seems to have no relation to the genera of the tribe Gratioleae and is situated close to the genera of the tribe Digitaleae including *Rehmannia.* I have treated this genus as a member of the tribe Gerardieae (Yamazaki 1985), but it seems better to treat this genus as a member of the tribe Digitaleae.

I am greatly indebted to Prof. D. Hartl, Johannes Gutenberg Univ., Mainz for his suggestion. He kindly sent me the paper of Dr. G. Vetter (Vorarbeiten zu einer Monographie der Gattung *Lindenbergia* Lehm. Doctor thesis, Johannes Gutenberg Univ. 1979, unpubrished).

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アジア，アフリカの熱帯に広がる *Lindenbergia* 属はオオアブノメ連 Tribe Gratioleae に入れられることが普通である。この連が属すゴマノハグサ亜科のものはつぼみの時花冠の上唇が下唇を覆うのが特徴の一つであるが，*Lindenbergia* は上唇が下唇で覆われる。この性質はシオガマギク亜科の特徴である。D. Hartl は *Lindenbergia* の研究を基礎に，花冠裂片の重なり方は重要なものでないとして，この特徴を重視した従来のゴマノハグサ科の体系とは別の体系を提唱した (Hartl 1957, 1965)。そして *Lindenbergia* はやはりオオアブノメ連に属させるのが妥当であるとしている。しかしゴマノハグサ科でのつぼみの時の花冠の重なり方は下唇の発達と関係し，送粉昆虫の足場を確保するために下唇の拡大の方向へ進化しているこの科では重要な特徴と考えられる。

オオアブノメ連の多くの属（サギゴケ属，アゼナ属，ミゾホオズキ属，アブノメ属，シソクサ属など）では花柱の先は平たい2片に裂け，受粉前の花では日当りのよい時に

この裂片が上下に広く開いている。この開いている裂片の内側をつつくと急速に閉じる。昆虫の体から花粉を受け取るための手段と考えられる。*Lindenbergia* の花柱の先は頭状であって，上記の受粉手段とは無関係な構造である。胚乳の出来方はオオアブノメ連のものとは関係なく，やや異なるがジオウ属のものと似ている。花冠裂片の重なり方，花柱の先の形などから考えて，*Lindenbergia* はシオガマギク亜科のジオウ属を含むジギタリス連に属すものと考える。この連の中では特殊化の進んだ属である。

○四国のカワヤナギ（山中二男）　Tsugiwo YAMANAKA: *Salix gilgiana* Seemen in Shikoku

カワヤナギ（*Salix gilgiana* Seemen）の分布は，四国の川原や湿地の植生をしらべユいて，以前から気になっていたことの一つである。このヤナギは四国にも自生することになってはいるが，どうも疑問に思えたので，そのことを木村有香先生におたずねした。すると，先生のところには九州の標本はないが，四国のものは1枚だけあるというご返事と，その標本のゼロックスコピーをいただいた。

四国の標本には，土佐国土佐郡鴨田村河ノ瀬で吉永虎馬氏が1934年9月9日に採集されたラベルがある。河ノ瀬（ごうのせ）は鴨田村ではなく潮江村で，1926年に高知市に入っているから，おそらくそこと鴨田村（1942年に高知市に合併）との境のあたりで採られたものと思う。それからちょうど50年後の1984年のおなじ日は，やはり日曜日で，何度か歩いたことのある高知市河ノ瀬町とその周辺をあらためてくわしく見てまわった。しかし，環境もすっかり変わって，カワヤナギを見ることができなかった。

その後，気をつけてみると，四国ではカワヤナギがよく栽培され，野生状のものも各県で見られることがわかった。いま手もとにあるカワヤナギの標本のうち，野生状態とみなして採集したところをあげると，徳島県鴨島町知恵島，川島町城山，香川県満濃町岸ノ上と真野，愛媛県砥部町宮内，宇和町坂戸と下坂戸，高知県野市町仁尾島と深渕がある。

だが，これだけで，カワヤナギが四国にも自生していたとは断言できそうにない。かつての河ノ瀬もそうであったと思うが，カワヤナギが生えているのはおもに人家の近くである（図1）。徳島県の吉野川や高知県の物部川の川原にもあるが，ジャヤナギ，アカメヤナギまたはタチヤナギのように普通ではなく，個体数もきわめて少ない。近くやおなじところにコリヤナギ，トキワサンザシ，ナンキンハゼなどが野生化していることもあり，カワヤナギもそれらと同様に，逸出の可能性が大きいことを否定できない。たしかに四国まではあるが，九州に分布していないヤナギには，バッコヤナギ，オノエヤナギそれにヨシノヤナギがあり，カワヤナギもおなじように四国には自生していてもお